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unit of genetic segregation; it is of unknown nature, but probably consists of a genetically indivisible portion of a chromosome (a *locus*) in a particular state.

The presence-and-absence scheme of factor notation properly employs only the first of these meanings; the Morgan-Castle scheme, on the other hand, may use either.

HOWARD B. FROST

CITRUS EXPERIMENT STATION,
RIVERSIDE, CALIF.

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THE SELECTION PROBLEM

UNLESS history fails to repeat itself, geneticists, whose attention is focused upon variation, should sooner or later overemphasize its importance as a factor in shaping the organic complex. There is, indeed, reason to believe that already a tendency for some among them to do so is becoming apparent. Dr. Pearl's[1] recent paper under the title above affords an example in point.

In that communication its author fails to discriminate sharply between two distinct phases of his subject. Whether selection may affect the course of evolution is a matter entirely apart from the possibility that it alters the germ plasm. Racial history may possibly be modified, if the genetic composition of a mixed population may be affected by selection based upon somatic differences. But modification of the germ plasm by selection is impossible, if that agency acts only as "a mechanical sorter of existing diversities."

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[1] Pearl, Raymond, 1917, "The Selection Problem," THE AMERICAN NATURALIST, Vol 51, pp. 65–91.

The present note is not concerned with the causes of variation. It refers only to the first-mentioned phase of the selection problem. It accepts the statements in the quotation below as substantially correct, and attempts in brief compass to evaluate the arguments by which Dr. Pearl supports his position regarding them.

By transposition of a few phrases his ideas may be expressed in his own words as follows:

> The mere fact of elimination and survival . . . is capable, in theory at least, of bringing about evolutionary changes of a progressive sort, . . . if the elimination be selective, and the survivors transmit to their progeny those differences that mark them off from the eliminated. The theory that these two rules are always and everywhere in operation, taken together with the observed fact that living creatures do die, *is* the Darwinian theory of Natural Selection as a factor in organic evolution.

If, as is implied, Darwin gratuitously assumed the intolerable burden involved in the use of the words, *always* and *everywhere,* it is immaterial. It is not a vital issue whether the form in which he expressed himself will bear literal interpretation, but merely whether his idea is correct that natural selection effects notable changes in the course of evolution. Hence it seems sufficient to say, that if the "Dance of Death" is governed in general, or even in part, by the joint action of the two principles enunciated in the preceding paragraph, the changes described there should follow as surely, although more slowly, than if the conformity were complete.

It is stated by Dr. Pearl, as one of three broad facts on account of which natural selection is no longer regarded as a primary, or perhaps even a major factor in evolution, that even when selective elimination on the basis of somatic characters does occur, it does not follow generally and regularly that the somatic differences on which the selection acted will reappear in the progeny, . . . actual experience having abundantly demonstrated that a very great many of such somatic differences are not inherited.

This may refer, first, to the fact that a single phenotype may include members of different genotypes. Yet, even so, no strict limitation is placed upon the possibility of changing the character of a mixed population by selection based upon somatic qualities. If plus variants of an inferior strain seem superior to individuals of a higher order of genetic worth, this will have its due effect in impeding progress; but since the essential point is, that, collectively considered, members of different pure lines do, in general, rather definitely reflect their different germinal constitution, advance may undoubtedly be made. However, it is unnecessary to labor the point, as it is not only admitted, but is urged by geneticists themselves in explanation of such results, for example, as those Castle and Phillips[2] obtained in selection experiments with hooded rats.

Reference to the genetic behavior of such characters as side-sprig of the comb in poultry may also be included in the quotation above. If, in this case, emphasis is laid upon the fact that selection might apparently be exercised indefinitely without the least tendency toward evolution of a side-sprigged race, it needs only be pointed out that the argument is directed against the contention that selection is capable of modifying the germ plasm. It has no bearing whatever upon the possibility of its occurrence in nature, nor, aside from the point indicated, upon its influence in evolution.

Upon the other hand it seems quite impossible that even if characters of which side-sprig is representative were highly useful, they should fundamentally modify the course of evolution under selection, or place any notable obstacle in its way, for they are not germinal variations and are as likely to occur in one line of descent as another. Hence, other things being equal, it is quite as probable that they should assure the survival of a subnormal representative of a superior genotype, as that they should tide over a superior representative of an inferior one; and the chance would be no greater that the attribute in question should appear in the offspring of one rather than in that of the other.

A second of the three general groups of facts to which reference has been made is summarized in the statement:

> Observation indicates that in many cases evolutionary changes have come about by relatively large, discontinuous steps, the new form being not merely fully differentiated at its first appearance, but also fully able to survive.

In another connection it is stated forcefully by Dr. Pearl that if the game of survival is actually played by the quoted rules he formulates (and no others are necessary) the conclusion is logically irresistible that progress is bound to occur in the direction of those differences which distinguish the survivors. But since obedience to his two rules is not in the least contingent upon the magnitude of the variations upon which selection is based, it must be admitted that the facts summarized above are entirely irrelevant to the present discussion. They neither bear upon the phenomena of inheritance, nor add anything to our knowledge of selective elimination.

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[2] Castle, W. E., and Phillips, John C., 1914, Carnegie Institution of Washington, Publication 49. Castle, W. E., 1916, "Genetics and Eugenics," Harvard University Press, Cambridge, 8vo, pp. vi + 353.

The third general fact cited in support of Dr. Pearl's contention regarding the diminished esteem in which natural selection is held as a factor in evolution is:

> All organisms possess in varying, but usually in very large, degree the power of personal, immediate, individual, somatic adaptation to the environment.

It is affirmed in addition, that in consequence of this power of personal adaptation the survival expectation of an individual is not generally and regularly a function of any static, single-valued relation between its somatic structure, habits or physiology, on the one hand, and the impinging environmental stresses on the other. Yet, it is asserted, such a relation is implicitly assumed in that part of the theory of natural selection which affirms a selective elimination on the basis of somatic characteristics.

The reply to these various statements is, that their substantial truth may be admitted without the possibility that evolution is affected by selective elimination being thereby in the least diminished. The adaptive capability of any individual either rests upon or lacks a germinal basis. In the former case there is no obvious reason why it should not itself provide material upon which selective elimination might be based, with consequent change in the composition of the population. In the latter, individual adaptability is as incapable of exercising influence upon the course of evolution, as side-sprig should be, if it were a useful character of the same order of importance.

If the accumulated results of genetic research provide no more effective arguments than these, it must remain an open question whether natural selection is not a primary factor, not in the *origin* of species, but in the determination of the elements composing the flora and fauna of the world at any period in its history. In other words, one who wishes to force an abandonment of that position must demonstrate that selective elimination does not occur upon such a scale that it may account for the results ascribed to it.

For many legitimate reasons Dr. Pearl has not treated this point at length in his article under discussion. But from the scanty evidence available he derives the following conclusion:

In some cases natural elimination is certainly in some degree selective, while in other cases it certainly is not, and in the most favorable cases of all the selection is apparently not very rigorous. Gross teratological abnormalities are eliminated. But the smaller deviations from type, which in theory ought to furnish the basis of selection, appear upon quantitative study less generally and sharply determinative of survival than might have reasonably been expected theoretically.

It is perhaps worthy of note that ever since it appeared that the larger, and rarer, discontinuous variations are in no danger of being lost through swamping, it has been beside the mark to ascribe especial theoretical significance to smaller deviations from type. Attention may also be directed to the important admission that in some instances elimination is known to be selective. It will then be in order to examine reports of researches upon the basis of which it is confidently asserted that in other cases the same is not true.

It happens that with five others one is cited which falls squarely within my own field of investigation. This is Professor Reighard's[3] "Experimental Field Study of Warning Coloration in Coral-reef Fishes," which Dr. Pearl seems to consider of particular significance for his own argument. But since it has been my good fortune to study the same material in the same place, more extensively and with better facilities, I feel justified in saying that Reighard's results will bear no such interpretation as is here placed upon them. He proved that gray snappers possess powers of discrimination and of memory which would lead one to suppose that, if the bright colors of the smaller reef fishes possess a warning significance, the snappers should be aware of it and avoid them. He did not prove beyond possibility of doubt that they do attack such fishes freely, but that is of no importance in the present connection; his conclusion that tropical fishes are not warningly colored with reference to their commonest enemies is perfectly sound. His ideas regarding immunity coloration are, however, the only ones in his paper which have the remotest bearing upon the matter of selective elimination, and there is no reason to suppose that these are more than logical deductions from incorrect premises.

Dr. Pearl's[4] own report upon the natural elimination suffered by barred (Plymouth Rock) and black, or near-black, chickens living under the same conditions is also mentioned. In this paper photographs show the black fowls looming up against natural backgrounds much more distinctly than do the barred. This is accepted as "objective and unbiased evidence regarding the relative conspicuousness of the two types of plumage pattern." It follows naturally, since the extensive record shows little difference in the rate of elimination of the two sorts of birds, that "the relative inconspicuousness of the barred color-pattern afforded its possessors no great or striking protection against elimination by natural enemies." But photographs serve as *accurate* measures of the conspicuousness of the fowls in the eyes of color-blind enemies only. Therefore, if rats and predaceous birds are not color-blind, and there is perfectly good reason for supposing that creatures lower in organization than either have color vision, it is not at all certain that the elimination in the two cases does not correspond fairly well with the actual difference in conspicuousness of the two types.

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[3] Reighard, Jacob, 1908, "An Experimental Field-study of Warning Coloration in Coral-reef Fishes," Carnegie Institution of Washington, Papers from the Tortugas Laboratory, Vol. 2, pp. 257–325.

[4] Pearl, Raymond, 1911, "Data on the Relative Conspicuousness of Barred and Self-colored Fowls," THE AMERICAN NATURALIST, Vol. 45, pp. 107–117.

Kellogg and Bell's[5] interesting "Studies of Variation in Insects" deals with 24 species. In 23 of them, including the lady-beetle, *Hippodamia,* to which Dr. Pearl refers, the authors show that there is much variation in individuals which have successfully run the gauntlet of natural selection. But since they have no knowledge whatever of the variation in the original populations, of which they have studied survivors only, these their results show nothing regarding the extent, or even the occurrence, of selective elimination.

In the honey bee alone duplicate studies were made of the variation of certain structures in individuals which were about to hatch, and in others, apparently from the same hive, after exposure to the vicissitudes of an active life. Among 200 drones in the first group the veins of the fore wings in 11 were imperfectly developed, and as a result normal flight became difficult or impossible. The variation in others of the first series seems essentially the same as that observed in the 300 members of the second, among which none of the defective individuals were found. But if these facts prove anything, it seems to be that selective elimination does occur when unfavorable variations affect the normal functioning of an organ. Suggestion is entirely lacking that the mechanical efficiency of the wing is impaired by the other variations noted, and it can scarcely be considered a pregnant fact, in the present connection at least, that indifferent variations provide no basis for selective elimination.

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[5] Kellogg, V. L., and Bell, R. G., 1904, "Studies of Variation in Insects," Proc. Washington Acad. of Sciences, Vol. 6, pp. 203–332.

In the same two series of bees the variation in the number of hooks upon the costal margin of the hind wings was determined without significant difference appearing in the two cases. In this instance, since the hooks appear to operate to the insects' advantage in binding the fore and hind wings of each side together, it seems plausible enough at first glance, that the more hooks there are the more efficiently their function will be discharged. Upon second thought, however, a difficulty suggests itself. The number of hooks varies from 19 to 29 in different individuals, but even the smaller number may, for all that is known to the contrary, perform perfectly the function ascribed to them. In that event the others are superfluous and the advantage they confer entirely fictitious. But waive the objection, and what follows? Simply a conclusion which in its relation to the present argument is already invalidated: Variations of the *magnitude* indicated provide no "handle" for natural selection.

It is unnecessary to carry the examination of the evidence farther. The three papers which have been reviewed are not carefully selected for criticism, but are the last, and apparently the most important, of six certified to be "fairly representative." If, however, this characterization is correct, it is apparent that the case against selective elimination is greatly exaggerated.

In conclusion, it appears that neither genetic research nor studies upon elimination closely limit the possibility that selection has played a very important part in evolution. In addition, recent field-studies[6] demonstrate novel facts of common occurrence which must apparently be ascribed to the action of this factor. Hence as was suggested in the beginning, Dr. Pearl would seem to over emphasize the importance of variation, and to attach too little significance to selective agencies in determining the course of racial history.

W. H. LONGLEY

GOUCHER COLLEGE,
BALTIMORE

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[6] Longley, W. H., 1914, Report upon color of fishes of the Tortugas Reefs, Carnegie Inst. of Washington, Year Book No. 13, pp. 207–208; 1915, "Coloration of Tropical Reef Fishes," Carnegie Inst. of Washington, Year Book No. 14, pp. 208–209; 1916; "The Significance of the Colors of Tropical Reef Fishes," Carnegie Inst. of Washington, Year Book No. 15, pp. 209–212; 1916, "Observations upon Tropical Fishes and Inferences from their Adaptive Coloration," *Proc. Nat. Acad. Sciences,* Vol. 2, pp. 733–737.